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LITTER MASS-LOSS RATES IN LATE STAGES OF DECOMPOSITION
AT SOME CLIMATICALLY AND NUTRITIONALLY DIFFERENT PINE SITES - A
STUDY ON THE EFFECTS OF CLIMATE CHANGE.

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SUMMARY

Berg, B., McClaugherty, C., and Johansson, M. 199X. Litter mass-loss rates in late stages of decomposition at some climatically and nutritionally different pine sites - a study on the effects of climate change.

The patterns of some chemical changes and litter mass-loss rates were investigated for a variety of decomposing litters in pine forests under different climatic conditions and at sites with different nutrient status. A mixed deciduous forest was also compared.

In initially chemically identical Scots pine needle litter incubated under different climatic conditions the lignin concentration increased faster, as a function of accumulated mass loss when the climatic conditions promoted a higher initial mass-loss rate. Also under artificially created conditions, e.g. after fertilization and irrigation, the same phenomenon occurred.

Litter mass-loss rates decreased during decomposition as lignin concentrations increased. The relative decrease was significantly larger at sites with a climate that promoted an initially higher mass-loss rate. At the same lignin concentration, however, the mass-loss rate was significantly lower in drier and colder conditions, viz. climatic conditions that promote a lower initial mass-loss rate. Nevertheless, it was found that at very high lignin concentrations that lignin clearly dominated over climate as a rate-regulating factor.

The authors speculate about that a consequence of this observation could be a higher rate of organic-matter accumulation at sites that initially promote a high initial mass-loss rate for litter than at sites with conditions that give lower initial rates, at least for a given species of litter.

Key words; litter, leaf litter, needle litter, mass loss, decomposition, lignin, chemical changes, climatic transect, fertilization, rate-regulating factors, effect of climate change.

INTRODUCTION

When plant litter is shed each litter type can have a different composition of both inorganic nutrients and organic-chemical compounds. During the process of decomposition the chemical composition of litter changes; the more easily available compounds are decomposed first and the more resistant compounds become more concentrated (Berg et al., 1982), giving the litter a progressively increasing recalcitrance (McClaugherty and Berg, 1987). In addition, recalcitrant lignin-like compounds are formed during the decomposition process (e.g. in the form of humic acids) (Stevenson, 1987) and many decomposing litters exhibit an increase in the amount of recalcitrant substances which they contain.

Due to their low rate of decay, lignin and lignin-like compounds have long been considered to exert a negative effect on the decomposition rate (Fogel and Cromack, 1977). Berg and Staaf (1980) proposed two phases in Scots pine needle litter decomposition; one initial phase regulated by the litter's concentration of the main nutrients and a later phase in which decomposition rate was ruled by the mass-loss rate of lignin.

This rate-regulating effect of lignin in a later phase has since then been generalized to some other needle and leaf litters (McClaugherty and Berg, 1987; Berg and Lundmark, 1987). Based on the progressively increasing recalcitrance of decomposing litter Berg and Ågren (1984) have estimated a theoretical final mass-loss rate for a given litter type in a given system based on the quality of the litter in a very late stage of decomposition (that is, in the humus stage). This final rate of decomposition was reached well after the onset of the lignin-regulated phase.

Soil moisture and soil temperature have a strong influence on litter-decomposition rates and in early stages of decomposition their influence may be estimated (Jansson and Berg, 1985). The interaction between rate-regulating factors, such as the litters' content of nutrients and lignin and other factors such as soil temperature and moisture have been investigated only

to a limited extent.

As regards the interactions, Flanagan and Veum (1974) studied respiration from some different litter types of different ages under a variety of temperature and moisture regimes. Their study indicated that the effect of temperature and moisture on respiration rate was less pronounced in older, more recalcitrant litter than in fresh litter. Meentemeyer (1978) developed some relations between the climatic index "actual evapo-transpiration" (AET) and the litter's lignin concentration and later Meentemeyer and Berg (1986) described relations for mass-loss rates of pine needle litter as compared to AET and to the litters' concentrations of nitrogen and phosphorus. Of these investigations the former did not discriminate between early and late stages and the latter dealt only with the early stages. The possible interaction between soil climate and the litter concentration of lignin as rate-regulating factors during late stages of decomposition has received little study.

The present synthesis paper has two aims. One is to show that the increase in concentration of lignin during litter decomposition varies with the ecosystem where the litter is incubated and with the litter's own nutrient status. The other aim is to find and establish differences in the rate-regulating pattern of lignin for one litter type incubated under different climatic conditions, which could illustrate effects of a climatic change.

SITE DESCRIPTIONS

Studies were carried out intensively at eight sites, (denominated 2,3,4,6,8,13, M, and B.I.) which are described in detail below. For 10 sites (Nos 10, 100 - 108) at which the studies were less intensive only the main site characteristics are presented in Table 1 and below. The site numbers correspond to those previously given by Berg et al. (1986;1991a). Further plot and site data are given by the references indicated in Table 1.

All sites except for the Blackhawk Island site (B.I.) had Scots pine (Pinus silvestris L.) monocultures. The Malung site (M), in addition, had lodgepole pine (Pinus contorta Dougl.) monoculture plots. Five of the intensive sites, namely No 2 (Harads), No 3:1 (Manjärvi), No 6:51 (Jädraås), No 8 (Nennesmo), and No 13 (Ehrhorn) were located on nutrient-poor, sandy sediment soil. The understory varied among the sites ranging from the Harads site (No 2) in the northern part of Sweden to the Ehrhorn site (No 13) in northern Germany. Site No 2 and plot No 3:1 had an understory composed primarily of cowberry (Vaccinium vitis-idaea L.) and lichens. The Jädraås site, plot No 6:51, was an 130-yr-old natural Scots pine forest and had as understory mainly bilberry (Vaccinium myrtillus L.), heather (Calluna vulgaris Hull) and mosses.

Site No 8 had an understory similar to that of No 6:51 with the exception that no lichens were seen. Also site No 13 had an understory similar to that of 6:51 but with some grass. All these sites had typical mor soils. For reference to more complete site descriptions see Table 1.

A group of sites situated close to one another and very similar in vegetation, soil type, and design (Nos 17, 18, and 19) have been combined in the present study and called M (Malung). The numbers 17, 18 and 19 which are used here as indices (Table 1) are those given by Berg et al. (1986; 1991a,b). These sites are relatively nutrient rich and had monocultures of either Scots pine or lodgepole pine with an understory of mosses and bilberry. They have been described in more detail by Berg and

Lundmark (1985;1987)

The Blackhawk Island site (B.I.) was different from the above sites since it was a mixed deciduous forest with a mull soil and with a dominant vegetation of sugar maple (Acer saccharum Marsh.) and very little understory. The site was relatively nutrient rich. A further site description is given by Pastor et al. (1982).

Sites 4 and 6 had experimentally modified plots. At the Norrliden site (No 4), the control plot (No 4:23) had a mor soil on till and was somewhat more nutrient rich than the poor sites, (e.g. 2, 3:1, 6, 8, and 13) and had bilberry and mosses as dominant understory. Plot No 4:29 had been fertilized with 120 kg N (as NH_4NO_3) $\text{ha}^{-1} \text{yr}^{-1}$ since 1971 and since 1974 the annual dosage has been 80 kg. In addition 40 kg of P and 76 kg of K were added in each of the years 1971 and 1976. The understory of the fertilized plot had changed accordingly and grasses and herbs suppressed the heather and bilberry.

The Jädraås site (No 6) had five plots with Scots pine, of which No 6:51 was a 130-yr-old forest, and plots Nos 6:15, 6:5, 6:4, and 6:17 were in a 30-yr-old forest in which the three latter plots were experimentally modified. At this site plots Nos 6:51 and 6:15 were natural and had as understory bilberry, heather, and mosses. The experimentally modified plots at site No 6 (Table 1) were either fertilized with 80 kg N (as NH_4NO_3) $\text{ha}^{-1} \text{yr}^{-1}$ (No 6:5) or irrigated with about 250 mm water (No 6:17) during the dry summer months, beginning in 1976. Thus increased the effective annual precipitation from the average 609 mm to about 860 mm (cf Berg et al. (1991c)). The understory in these modified stands had changed with respect to the control plot. For example the fertilized stand (No 6:5) lost its understory and the ground had only a cover of brown pine needles. The understory of the irrigated plot was composed of heather and mosses, of which the latter grew luxuriously. In contrast, plot 6:4 with irrigation and dissolved fertilizer had a dense understory of grasses, red raspberry (Rubus idaeus) L) shrub and fireweed (Epilobium angustifolium L).

Site No 3 (Manjärv) had three subplots which had different

nutrient status and different understory. No 3:1 had lichens and cowberry as well as some heather in the understory. No 3:2 was somewhat wetter and more nutrient rich and had bilberry and mosses as dominating understory. Subplot No 3:3 was the most nutrient-rich plot and was also wetter than the other two and the understory was dominated by grasses and bilberry.

The size and shape varied among the plots: at site No 2 the plot measured 10m x 30m; each plot on site No 4 was 30m x 30m; at site No 6 plot 6:51 measured 100m x 300m; all other plots at site No 6 were 30m x 30m; the plot of site No 8 was 40m x 40m; at site No 13 20m x 30m; all plots at site M measured 30m x 30m as did the plot of site B.I., and the plots Nos 3:1, 3:2, 3:3, 10:1 and sites 100 - 108.

Additional site information is given in Table 1 where also references are given to original site descriptions.

MATERIALS AND METHODS

Needle collection, storage and sample preparation

Litter types and denominations

In this study we used both local litter, collected and incubated at particular sites and a unified litter preparation of Scots pine needles, collected at a single site and incubated at many sites, as well as experimental litters. All Scots pine needle litter collected at the main stand at the site Jädraås has been called "unified litter". All litter that has been collected at the other different natural (control) sites and plots has been denominated local litter. Further, all litter collected at fertilized stands and all litter that has been transplanted to a site, other than its origin has been called experimental litter. An exception to this is, of course, the "unified litter".

Unified and experimental litters

Unified brown needle litter was collected from a single stand at abscission each year (late September) by gently shaking the branches. The stand was 15 years old when the study began in 1973. This "unified" litter was collected at the research site of the Swedish Coniferous Forest Project (Jädraås, site 6; Appendix 1). All trees sampled were located in an area less than a hectare. Green Scots pine needles were collected in the same area and taken during winter as 2- and 3-year-old needles (Berg and Ekbohm (1991). Experimental Scots pine needle litter was collected during litterfall at the experimental plot Lisselbo (LISS), a fertilization optimization study plot (Tamm et al., 1974; Berg and Staaf, 1980). The collection and decomposition of these needle litters has been described earlier by Berg et al. (1987). Lodgepole pine needle litter was sampled at site No M:17. This sampling has been described by Berg and Ekbohm (1991).

Local litters

Local, brown needle litter was, in addition, sampled at sites B.I. and Nos 2, 3, 4, 6, 10:1, 100-108, and sites M:17-19. These samplings took place at time for abscission.

Sample preparation

The sampled litter was air dried and stored dry at room temperature until sample preparation took place. Before weighing, the needles were allowed to equilibrate at room temperature to a constant moisture level, approximately 5-8 %. For a given sample the largest difference in moisture was less than ± 0.5 %-units from the average as determined by 20 or 25 samples.

Experimental design, incubation and mass loss determination

At all sites except for site B.I., litter samples were incubated in a randomized block design at 25 spots within the plot. The procedures of incubation and sampling of litterbags were very similar among the plots of sites Nos 2-8,10:1,13, 100-108 and site M, but more detailed descriptions have been published (Berg et al.,1991c; Berg and Lundmark,1987, Berg et al., 1982). The design for sites Nos 10:1 and 100-108 has been described by Johansson (1986) and for site B.I. by McClaugherty and Berg (1987). At the B.I. site litter samples were located completely randomly along transects within the plot.

Each incubation spot measured about 1m x 1m. At all sites the samples were placed on the A_{oo} layer and incubation time was up to five years with samplings normally 2-3 times a year.

When collected (one sample from each incubation spot), the samples were transported directly to the laboratory and cleaned of mosses, lichens and other remnants of ingrown plants. After the removal of plant remains, the loss of dry mass of the needles was determined by drying the samples to a constant mass at 85°C (50°C for the B.I. site). Mean values of mass loss were calculated for each sampling (n=25 at all plots except for site B.I. with n=4 to 10). After this the samples were combined for chemical analysis.

Chemical analysis

Sites Nos 3,4,6,8,13, and M.

The combined samples were ground in a laboratory mill equipped with a screen allowing particles of less than 1 mm to

pass. The amounts of water-soluble and ethanol-soluble substances were determined by sonicating the milled sample three consecutive times with fresh solvent in a sonicator bath and weighing the samples after filtration and drying. The analyses for sulfuric-acid (Klason) lignin in the needle litter samples were carried out according to Bethge et al. (1971) (see also Berg et al., 1982). Nitrogen was determined by a semi-micro-Kjeldahl method using a flow-injection analysis apparatus (Bifok FIA 05, Tecator, Höganäs, Sweden) with gas diffusion and using phenol red as an indicator (Svensson and Anfält, 1982). For analysis of phosphorus, sulfur, magnesium, calcium, potassium, and manganese, samples were digested for 2 days in a 2.5:1 (v/v) mixture of nitric and perchloric acid. The analyses were performed by plasma atomic-emission spectrometry ICP-AES (Instrumentation Laboratory IL P-200, Andover, Massachusetts, USA).

Sites Nos 2, 10:1, and 100-108

For the samples from these sites the following procedure was used. After a wet oxidation in H_2SO_4 , total nitrogen was analyzed using a semi-micro Kjeldahl procedure (Nihlgård, 1972) and phosphorus by a molybdenum-blue method (John, 1970). Potassium, calcium and magnesium were determined by atomic adsorption spectrometry (Perkin-Elmer 603) against acid standard (Pawluk, 1967). For calcium and magnesium, the analyses were made in a 0.3 % $LaCl_3$ solution. These analyses were carried out at the same laboratory as those of the above sites and the resulting values were compatible. Lignin analysis was carried out as described above.

Site B.I.

The ground samples were extracted with dichloromethane (Anonymous, 1976), followed by hot water (Anonymous, 1975). Holocellulose and lignin were determined in the extract-free residue in a two-stage digestion with sulfuric acid according to the method of Effland (1977). Total nitrogen was determined using a sulfuric acid-hydrogen peroxide digestion followed by

analysis of ammonium with a Technicon Autoanalyzer (Anonymous, 1977). Reanalysis of site B.I. litters using the above sulfuric-acid lignin method indicated that the results from both methods are essentially identical (McClaugherty and Berg, 1987).

Initial chemical composition of the litters used

Initial chemical composition of the litter has been described elsewhere for most of the litters but are here collected in Appendices 1 (unified litter) and 2 (local and experimental litter) where literature references are also given.

Data on litter mass loss and chemical changes

All basic data used for the calculations have been printed in reports. For the sites Nos 2,3,4,6,8,10:1,13,100-108 and M data are found in a report by Berg et al. (1991b), and for site B.I. in a report by Aber et al. (1984).

Terminology

We have used the word lignin to mean sulfuric-acid (Klason) lignin (non-hydrolyzable in sulfuric acid), being aware that the terminology is not entirely correct as the fraction analysed for includes, in addition to native lignin, some humic compounds as well as some ash. The chemical similarity of lignin and humic compounds is supported by the study of Norden and Berg (1989), who found no deviations in ^{13}C NMR adsorption spectra in a series of partly decomposed needle litter samples. We thus have used the term lignin here for the sake of simplicity.

In order to have an easily handled expression for the slope of the linear equation giving the increase in lignin concentration as a function of accumulated percent mass-loss, we have used the acronym LCIR with the meaning "Lignin Concentration Increase Rate".

Conditions for selecting data

For the analysis of the variation of lignin concentration with accumulated mass loss we used only decomposition sets

that had reached well into the late phase of decomposition, namely sets with an accumulated mass loss of at least 45 percent. Although the choice of 45 percent accumulated mass loss was arbitrary, we selected it so as to include only those data sets which had entered a stage of decomposition in which lignin concentration entered a rate-regulating stage.

In the calculations of decreasing mass-loss rate with increasing lignin concentrations we used only decomposition data from litter that was in a late decomposition phase, namely in a stage where the concentration of lignin ruled the litter mass-loss rate (Berg and Staaf, 1980; Berg et al., 1987). All the litter types that were used were considered to have reached this stage by the time that they had lost at least 20 percent of their initial mass, so we used only data for materials that had decomposed at least that far.

RESULTS

Overview and general comments

We first investigated differences in lignin concentration increase rates (LCIR) using several data sets with data from:

- 11 sets of one litter type (unified litter) decomposing at one site. This was done at site No 6:51. (Table 2, Appendix 3a, Fig 1).
- one litter type (unified litter) at five climatically different, nutrient-poor sites (Nos 2,3:1,6:51,8, and 13)(Tables 2 and 4, Appendix 3a,b, Fig 2).
- local Scots pine needle litter at three plots of different nutrient status (Tables 3 and 4).
- unified and experimental litters at some sites of different nutrient status including fertilized plots (sites Nos 3,4, and 6; Tables 4 and 5).
- local Scots pine needle litter at several different sites (17 sites, Tables 3 and 6).

We further analyzed the change in decay rate of litters as dependent on changing lignin concentration during decomposition using:

- unified litter at one site (No 6:51)(Table 7)
- unified litter at five climatically different Scots pine sites which were nutrient poor (Nos 2,3:1,6:51,8,13;Fig 3).
- local litter at different sites (Table 7, Figures 4 and 5).
- unified litter incubated in fertilized and manipulated Scots pine stands (sites Nos 4, and 6; Figure 5).

The variation in the litters' lignin concentration vs accumulated litter mass loss - Scots pine needle litter

Variation within one site (No 6:51)- unified Scots pine needle litter.

When the lignin concentration increases during litter decomposition the increase vs accumulated mass loss may be described as a straight line up to relatively high mass-loss values (cf. Berg et al., 1984). A noticeable general phenomenon was that all needle litter types had slow and smooth increases in lignin concentrations as decomposition proceeded (Berg and Ekbohm, 1991). A linear regression for all sets of unified litter incubated at this site using 104 value pairs gave a straight line with a slope of 2.970, and an r^2 value of 0.869 (Fig 1; Table 2). When comparing the increase rates in lignin concentration (LCIR) for individual litter sets we found that the slopes for chemically similar litter sets of unified litter incubated during different time periods at site No 6:51 ranged between 2.30 and 3.81 (Appendix 3a).

Variation among five, climatically different Scots pine sites of similar nutrient status - unified Scots pine needle litter (sites Nos 2,3:1,6:51,8, and 13)

LCIR values were compared for unified Scots pine needle litter incubated at five climatically different sites (Table 1; Fig 2). Sites Nos 8 and 13 had on the average warmer, and wetter climatic conditions, than did the sites 6:51, 3:1, and 2, thereby promoting conditions for a higher initial decomposition rate. Under these conditions lignin concentrations increased rapidly versus accumulated mass loss with the LCIR slopes of 3.90 and 4.04 respectively. These slopes were steeper than those at sites Nos 2, 3:1, and 6:51, where the slopes were 2.48, 1.97 and 2.97 respectively (Fig 2; Table 2). The basic equations used were all clearly significant straight lines (cf Appendix 3a and b) and only unified Scots pine needle litter was used in the comparison.

The steepest slopes were observed at the two sites with the highest temperature and precipitation (Nos 8 and 13). The values for the LCIR's, while not significantly different from one another, were significantly greater than those from the other sites. At the other extreme were the slopes for LCIR at the sites with lower temperatures and lower precipitation (Nos 2, 3:1, and 6:51) more shallow, which indicates a difference between the more moist and warm sites and the more cool and dry ones.

The effect of climate or site on lignin-concentration increase rate - local Scots pine needle litter, several different sites.

At the site Manjärvi (No 3) the three nearby Scots pine plots (located within a radius less than 100 m) had different hydrology and different nutrient status as indicated by soil properties and the ground vegetation. The driest site (No 3:1) had lichens, sparse and low cowberry shrub, and low initial decomposition rates. Plot No 3:2 which was wetter had bilberry shrub indicating a higher nutrient status. It also had a higher initial mass-loss rate for pine needle litter. The LCIR value was significantly higher than for plot 3:1 (2.55 vs 1.97; Table 4). For plot 3:3, which was the most nutrient rich and wettest site and also had the highest initial mass-loss rate, the LCIR was even higher (2.83), but not significantly than that of plot No 3:2.

A data set was investigated to trace large-scale variations in LCIR values within one litter type for a wide range of climatic situations and sites. For each site we tested the linearity of lignin concentrations vs accumulated mass loss (Table 3). In all cases except one the significance was on the level of $p < 0.001$. With the observation (above) that natural sites with higher initial mass-loss rates (or at least a higher potential for a high mass-loss rate) also had higher LCIR values, we decided to use first-year mass-loss as an approximate site index for climate and nutritional conditions guiding decomposition rates.

As a first step we compared the values for LCIR (slope) and

first-year mass-loss values by simple linear regressions, investigating Scots pine needle litter only (Table 6) and using data from sites Nos 2,3:1-3, 10:1, and 100-108 which were all obtained in the same investigation. The data set used (Table 3) was a set independent of those tested earlier. A clearly significant positive relation was obtained ($p < 0.05$) indicating that there was a relationship between the site properties promoting a high initial decomposition rate and the LCIR values.

Since we had found that the lignin-concentration increase rate (LCIR) also varied with initial lignin concentration we made a linear regression of LCIR values versus initial lignin concentration as an independent variable. A clearly significant negative relation was obtained (Table 6) indicating that the higher the initial lignin concentration of the litter the slower the slope of the increase. Finally, a multiple linear regression was run using both lignin and first-year mass loss as independent variables which gave an r^2 value of 0.863 ($n=14$; $p < 0.001$). We thus may conclude that the increase rate of lignin was dependent on both site characteristics as reflected by the first-year mass loss and by the initial concentration of lignin. There was no correlation between initial lignin concentration and 1st year mass loss within this transect (Table 6).

In a second step we used a larger set of data including all unified and local Scots pine needle litter as well as that of white pine incubated in natural systems. The data set also covered a wider climate range (Table 6). When LCIR values were tested versus first-year mass loss a significant positive relation ($r^2 = 0.111$; $n=47$; $p < 0.05$) was obtained.

The relation between LCIR values and the litters' initial lignin concentration was highly significant and negative ($r^2 = 0.387$; $n=47$; $p < 0.001$). When the regression was run versus both mass loss and initial lignin concentrations the value for the correlation coefficient increased to 0.406 and the relation was still highly significant ($p < 0.001$; Table 6). To investigate for a possible correlation between 1st-year mass loss and initial lignin concentration a linear regression was run and none was found ($r^2 = 0.009$; $n=47$; Table 6).

A comparison of two different local needle litter types at their native sites

At site M the LCIR values were lower for lodgepole pine needle litters incubated in the lodgepole pine stand (1.24) than for those of Scots pine, incubated in the nearby Scots pine stand (2.55) (Table 8). The reason in this case is probably the higher initial lignin concentration in the local lodgepole pine needles (Appendix 3c) which is reflected by the intercepts being 370.6 mg g^{-1} for the lodgepole pine needles and 277.5 mg g^{-1} for the local Scots pine needles from the same site. The average slopes were significantly different and so were the intercepts.

Litter incubated under experimental conditions viz. transplanted litters and manipulated plots.

Transplanted litters - control plots

At each of the control plots Nos 4:23, 6:51, and B.I. several transplanted litter types were incubated in addition to the local litters and the LCIR values (slopes) were compared for different litter types incubated on the same soil.

At site 4:23 green needle litters with a high initial decomposition rate had a considerably higher LCIR value (steeper slope) than the brown needles that initially decomposed more slowly in the same plot (Table 5). With an LCIR value of 5.27 the green needles had an LCIR value almost twice that of the brown ones (2.99).

At site 6:51 we made a similar comparison and found that nutrient enriched brown needle litters collected from a fertilized site (site LISS; Table 1) and green pine needles incubated at site 6:51 showed very similar slopes (Appendix 3a). When measurement series were combined the experimental litters gave the higher LCIR value of 3.20; (SE 0.31; $n=65$) which was not significantly different from the slope of the unified litter (2.97; SE=0.11; $n=104$) (Table 2), even if the two slopes were not far from being significantly different. Thus, we did not obtain a clear answer to whether raised nutrient levels would affect the LCIR value.

At the same site (No 6:51) there was a variation in LCIR values within the site when litter types varied. For brown lodgepole pine needle litters which had high initial lignin concentrations the slopes were relatively low (Table 8) even if the slope for green needles was barely significantly steeper than that for the brown ones.

At site B.I. white pine needle litter gave a slope of 3.12 which was significantly lower than that of eastern hemlock needle litter (3.97). This shows that the data from site B.I. using different species of needle litter fit to the results shown in Figure 2 and Table 6. The climate (temperature and precipitation) of site B.I. is intermediate to those of sites 6:51 and site 8 and the slopes (above) thus fit well with the pattern indicated as indicated by climate alone. Further, the initial lignin concentrations of the two litter types (hemlock 206 and white pine 225 mg g⁻¹) also fit the observation that LCIR is influenced by initial lignin concentration.

So, we may conclude that both site characteristics and lignin concentrations in the litter were important factors in determining the increase rate in lignin concentration for a wide range of sites and litters and that lignin concentrations may be the dominating factor in that relation.

Variation between control plots and fertilized plots

Increase rates in lignin concentration (LCIR values) were compared for Scots pine needle litter in some fertilization experiments. Chemically identical needle litter was incubated at two different sites (Nos 4 and 6) where heavy dosages of nitrogen and phosphorus fertilizer had been applied. It was clear that the increase rate for lignin concentration (LCIR) in needle litters was significantly higher in the fertilized plots than in the controls. Thus, for brown needles at site No 4 the increase rates were 4.25 and 2.99, respectively and significantly different at a fertilized plot (No 4:29) and at a control plot (No 4:23) respectively (Table 5). Within the same plot, green needle litters gave higher slopes than the brown needle litters - in the control plot with 5.27 as compared to 2.99 and within the fertilized plot with 5.17 vs 4.25. In each of the cases the difference was significant. When combining all litters in the

control plot the slope of the control plot litters (3.77) was still significantly lower than that of the litters of the fertilized one (4.47).

At site 6 the LCIR values were 3.57 and 3.21 for unified Scots pine needle litter in the fertilized plot (No 6:5) and the control plot (No 6:15) respectively (Table 5). The litter incubated in the control plot was initially identical to that in the fertilized one. Irrigation only (plot 6:17) did not increase the slope whereas irrigation plus fertilization (plot 6:4) gave a steeper slope (4.87) which was significantly different from the LCIR values for other treatments at this site. In all those cases unified litter was compared.

Effect of lignin concentrations on mass-loss rate - late stages of decomposition

One site - one litter species (unified litter; site 6:51)

Lignin decomposition is a slow process, and consequently the decomposition rates of whole litter in late stages of decomposition are regulated so strongly by lignin that the climatic influence may be much less pronounced than in early stages (cf. Berg and Ågren, 1984; McClaugherty and Berg, 1987).

In order to focus on later decomposition stages we considered only data sets with > 20 percent accumulated mass loss, when lignin concentrations had increased enough to retard litter mass-loss rate (McClaugherty and Berg, 1987; Berg and Staaf, 1980). We examined the effect of lignin concentrations at the beginning of a one-year period on the mass-loss rates of the litter during that one-year period.

For one site (No 6:51) we tested the effect of lignin concentration on mass-loss rates in later stages of decomposition using unified Scots pine needle litters (Table 7; Fig. 3). The relation was highly significant ($r^2=0.478$; $n=29$; $p<0.001$). The annual mass-loss thus decreased from 30 percent per year at a lignin concentration of 320 mg g⁻¹ to 20 percent per year at a lignin concentration of 440 mg g⁻¹. For this site there are earlier reports on the retardation in mass-loss rate (Berg and Ågren,

1984;McClagherty and Berg, 1987) related to increasing lignin concentration.

Comparison of the decomposition rates for two different litters incubated at site 6:51.

At site No 6:51 (a mor site) data from two different types of incubated Scots pine needle litter were compared (Table 7); the unified litter and some sets of experimental Scots pine needle litter from fertilized trees. The two sets had initially different chemical composition as regards nutrients with the experimental ones having about 2-3 times as high concentrations of nitrogen, phosphorus, and sulfur as teh unified litter. When correlating annual mass loss versus the litter's lignin concentration at the start of each one-year period the experimental litter gave a steeper slope (-0.085) than the unified litter (-0.078) but the slopes were not significantly different. This indicates that for a given species and site the litter's nutrient composition may have a limited influence on lignin regulation of mass-loss rate.

Five climatically different sites (unified litter; sites Nos 2,3:1,6:51,8, and 13)

We compared the effect of lignin concentration on litter mass-loss rates for five sites that were climatically different but had similar nutrient status (Nos 2,3:1,6:51,8, and 13). For the five sites investigated, both the slopes were partly different and formed a pattern. The steepest slopes were those estimated for sites No 13 and 8 which both had the highest mean annual precipitations and mean annual temperature (Table 1) and consequently the highest initial decomposition rate. The slopes (-0.250 and -0.211 % ^a mg g⁻¹) were not significantly different but both were significantly steeper than the slopes from the other three sites meaning that the lignin concentration had a clearly stronger effect on mass-loss rate at these two former sites as compared to the other ones.

Litters incubated on sites Nos 2 and 3:1 had very similar slopes, whereas that of No 6:51 was clearly higher and significantly different from the other ones. Although the sites No 3:1 and 2 are cooler, they have a higher mean annual precipitation than site 6:51 (Table 1) but the initial decomposition rates are lower than at site 6:51. The effect of lignin concentration was significantly stronger for site 6:51 than for site No 2 (Fig 3) and we may distinguish mainly two groups of sites and an intermediate one. In fact, the influence on litter mass-loss rates was so low at the two cooler sites that the regression lines were so shallow that they were not significant. Thus, over a broad range of climates, decomposition rates were more sensitive to increases in lignin concentration at warmer, more mesic sites (e.g. sites Nos 8 and 13). The reason to a stronger effect of lignin may be connected to the faster increase in lignin concentration observed (cf Fig 2). A composition of the microbial population could be dependent on climate and we may thus speculate in that under cooler and drier conditions a higher proportion of the lignin was degraded giving litters at these sites a lower proportion of lignin and a higher proportion of celluloses. The litters that initially were being degraded more quickly could thus have a lower proportion of the lignin degraded. With a higher concentration of lignin resulting the remaining litter would thus be more recalcitrant.

The litter types used in the comparison were local Scots pine and unified litters (Fig. 3) which had initially rather similar concentrations of nitrogen and phosphorus as well as lignin (about 2.5-4.2 mg g⁻¹, 0.20-0.34 and 223-288 mg g⁻¹ respectively). The interval of lignin concentrations used in the linear regressions was similar among the sites (site No 2; 343 - 475 mg g⁻¹, site No 3:1 314.0 - 400.6 mg g⁻¹, site No 6:51; 315 - 442 mg g⁻¹, site No 8; 302 - 460 mg g⁻¹, and site No 13; 380-520 mg g⁻¹). A linear regression was also run to compare the slopes at site No 8 and No 6:51 using an interval for lignin concentration that was exactly the same for both sites. No change in slope was seen, although the correlation coefficients were somewhat lower.

Comparison of the decomposition rates for two different litters incubated at their individual stands (sites M).

At site M (a mor site) field incubations were made using local Scots pine and lodgepole pine needle litter and in both cases the mass-loss was followed to about 65-75 percent. For decomposition in the 2nd, 3rd and 4th years we tested the influence of lignin concentration on litter mass-loss rate for each species separately and found two significant linear relations (Fig 4). The relation for Scots pine needle litter was highly significant ($r^2=0.794$; $n=15$; $p<0.001$) whereas that for lodgepole pine needle litter was more diffuse even if significant ($r^2=0.289$; $n=16$; $p<0.05$) (Fig 4). The two straight-line relations were almost parallel and neither their slopes nor their intercepts were significantly different, though (Table 7).

Unified litter incubated in an experimental Scots pine stand (site 6; irrigated and fertilized stands)

In a manipulated forest at site No 6, two stands were compared at the same site, namely a control stand (No 6:15) and an irrigated plus fertilized (IF) stand (No 6:4).

In later decomposition stages (> 20 percent accumulated mass loss), decomposition rates decreased for litter in both the control stand and in the plot with a combined irrigation and fertilization treatment (IF plot) (basic data from Berg et al., 1991c). The effect of lignin concentration was significantly stronger in the IF plot (Fig 5) as the slope of the regression line between lignin concentration and annual mass loss was considerably higher (slope = -0.156 ; $r^2=0.849$; $n=9$; $p<0.001$) (Table 7) than that of the litter in the control plot (slope = -0.095 ; $r^2=0.652$; $n=16$; $p<0.001$).

The plot with combined irrigation and fertilization had conditions that raised the initial mass-loss rate for litter as compared to those of the control plot. It thus appears that in this manipulated plot we obtained results similar to those observed in a geographically long climatic transect.

DISCUSSION

Different increase rates in lignin concentration

That lignin concentration in decomposing litter increases with different rates may be explained by an interaction of factors limiting to the activity of the microbial decomposers and maybe a difference between microbial communities.

A likely interpretation is that under warmer and wetter conditions these two factors are less limiting, if limiting at all for the microbial community. This could mean that the fungi and bacteria decomposing the relatively easily degraded cellulose and hemicellulose had the possibility to invade the litters and degrade them at a higher rate. Lignin is less energy rich and thus not primarily attacked and thus degraded more slowly. Consequently climatic conditions that favour a high degradation rate of celluloses would not affect the lignin degradation to a comparatively high extent. This would thus mean a proportionally higher decomposition rate of the celluloses' fraction and a more quickly increasing concentration of lignin. Under soil climatic conditions that are less favourable *viz.* lower temperature and lower precipitation the difference in degradation rates between the celluloses on one hand and lignin on the other would be less and consequently the increase in lignin concentration would be relatively slower *versus* the accumulated mass loss.

This kind of interpretation may also be used to explain the relatively higher increase rates of lignin in litter that has higher nutrient levels (e.g. green needle litter) and the higher increase rates in lignin concentrations in litter in fertilized forest stands (Tables 2 and 5). Raised nutrient levels tend to enhance the decomposition rates of chemical components in litter like cellulose, hemicelluloses and soluble substances (cf Berg and Staaf, 1980) and the effect, in this case, would be a higher increase rate in lignin concentrations.

The present paper presents observations that have been made in ecosystems in which pines are the dominating species. In addition Berg and Tamm (1991) reported a similar observation in a Norway spruce forest. Even so, we may not conclude that this type of effect is general. The pattern of lignin dynamics

described here may not hold in systems with a high activity of soil fauna. Additionally, the soil microbial community could behave differently in other systems. For example, in soils that are dominated by microbial populations with the ability to utilize the energy in lignin, e.g. white-rot organisms, the pattern may be different.

Differences in the effect of lignin on mass-loss rates.

The concentration of lignin had increased more quickly (relative to accumulated mass loss) at the warmer and wetter sites (Fig 2) thus giving an effect on the litter quality which clearly could influence subsequent mass-loss rates. This possibly would be part of the observed effect and it appears reasonable to conclude that the influence of lignin on mass-loss rate was caused both by litter properties and climatic factors at each site. In an earlier paper Berg and Ekbohm (1991) observed at a given site (No 6:51), and thus a given climatic situation, that the faster the decomposition in the earlier stages the slower the decomposition in the later phase. This kind of empirical finding supports the discussion above that factors (in this case substrate quality factors) promoting high initial mass-loss rate (including the decomposition of cellulose) thus leaves higher lignin concentrations or the whole insoluble fraction more resistant. The strong effect on mass-loss rate at more warm and wet climatic situations could in part be influenced by the interaction of two counteracting influencing factors. With climate factors more optimal the effect of lignin could be seen more clearly. As lignin decomposition is a slow process, a consequence is that also the decomposition rates of whole litter in late stages of decomposition (say, at lignin conc $> 450 \text{ mg g}^{-1}$) are regulated so strongly by lignin that the climatic influence would be much less pronounced than in early stages (cf. Berg and Ågren, 1984; McClaugherty and Berg, 1987).

In a comparative study, lignin concentration could explain about 80 percent of the mass-loss rate for Scots pine needles in late stages ($r^2=0.801$) whereas the corresponding figure for lodgepole pine needles was 37 percent ($r^2=0.371$; Fig 4). It thus appears that for the latter needles, some other factor(s) may be more important in controlling the rate. Whereas for Scots pine

needles the concentration of lignin increased relatively quickly from around 200-250 mg g⁻¹ initially up to around 500 mg g⁻¹ as a final value (reached asymptotically, cf. Berg et al., 1984; Berg and Ekbohm, 1991) the lodgepole pine needles started with an initial value of around 380 - 390 mg g⁻¹ to reach about the same maximum value. The more narrow span for lodgepole pine needles may explain the greater scatter (and lower r² value) for this litter type.

The annual mass-loss rates for unified Scots pine needle litter measured at the control- and IF-plots were plotted versus concentrations of lignin at the beginning of each one-year period (Fig 5). In both cases highly significant linear relations were obtained with $r=-0.649$, $n=22$; $p<0.001$ (control plot) and $r=-0.972$, $n=6$; $p<0.01$ for the IF-plot. Although the litter mass-loss values for the IF-plot were clearly above those of the control plot at the same lignin concentration (Fig 5) the regression line for mass-loss rates of the irrigated and fertilized plot had a considerably steeper slope and a higher intercept than that of the control plot litter (Fig 6). Similar to the corresponding lines in Fig 3, the two regression lines converged and one might expect that at some point above a concentration of 500 mg g⁻¹ of lignin they may either cross each other or approach a common maximum value (cf McClaugherty and Berg, 1987). The steeper slope means that although the litter in the IF-plot had a higher initial mass-loss rate, mass-loss rates declined more rapidly at higher lignin concentrations than it did in litter on the control plot.

An observation which may be compared to the present one was made by Söderström et al. (1983). When measuring soil respiration rates in a set of nitrogen-fertilized plots they found a highly significant, negative effect of nitrogen amendments on microbial respiration from humus as well as on live bacterial biomasses (direct counts). The fixation of ammonia to organic material and the consecutive chemical reactions have been suggested to give rise to more recalcitrant compounds (Berg and Ekbohm, 1991). A higher initial mass-loss rate and consequently also mineralization rate may thus have that kind of effect (for a review see Nömmik and Vahtras, 1982). Products of lignin degradation may react with ammonia or amino acids to form

recalcitrant complexes (Bremner and Shaw, 1957). The results of laboratory experiments indicate that the concentration of ammonium/ammonia could be rate-limiting for this kind of reaction to proceed (Axelsson and Berg, 1988).

A further possible contributing factor is the observation by Keyser et al. (1978) and Kirk et al. (1978) who found that amino acids and ammonium ions repressed the formation of lignolytic enzymes in one fungal species. There now appear to be several species which have this kind of repression (P. Ander, pers. comm.). Although substrate quality and lignin in particular plays an important role in regulating litter decomposition rates, the pattern of changes in lignin concentration during decomposition can be significantly influenced by site factors such as climate and nutrient availability. The mechanisms underlying these observations and their applicability in other ecosystems have yet to be determined.

Provided that the finding of ligninase repression (above) is correct and reflects a more general phenomenon, and one could expect that higher amounts of mineralized and low-molecular nitrogen appear per time unit in connection with a higher turnover rate. This nitrogen may react with lignin remains, form recalcitrant compounds and thus decrease lignin degradation rate and consequently also litter mass-loss rate.

It is thus reasonable to assume that either one or both of these mechanisms may contribute to decreasing the decomposition rate of lignin. Such a mechanism may suggest that at sites with climatic and nutritional factors allowing high initial rates we may expect that an accumulation of partly decomposed litter may take place. Possibly such an accumulation would go at a higher rate there than at climatically more unfavourable sites.

Integration of the two phenomena described here, namely climatic and site quality influences on LCIR and the effect of lignin concentrations on mass-loss rates, goes beyond the scope of the present paper. Such an integration may prove helpful in understanding the dynamics of litter in later stages of decay as it approaches humus.

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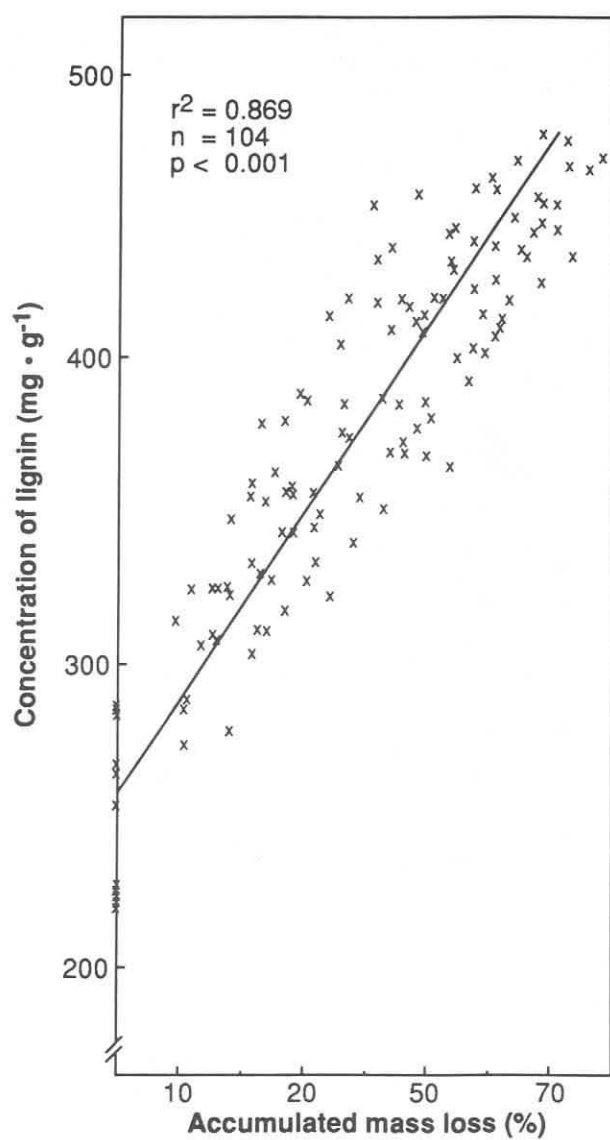


Fig 1. The increases in lignin concentration with accumulated mass loss for 11 sets of decomposing Scots pine needle litter incubated at the site of collection (No 6:51) with a mor soil. The linear regression line for the slope is given.

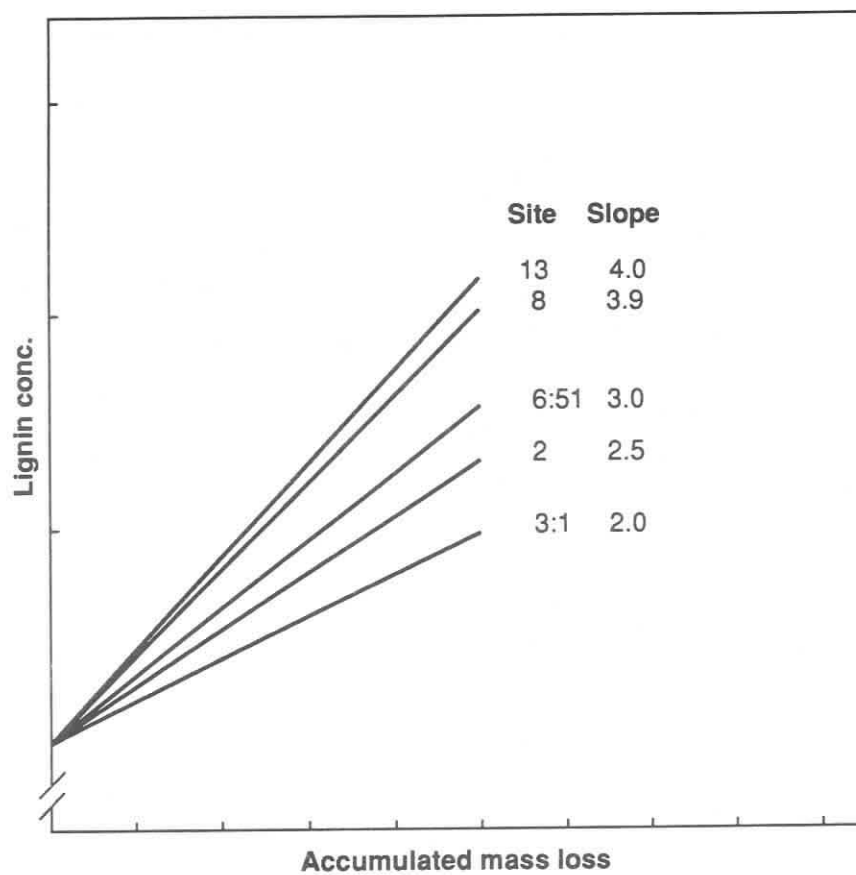


Fig 2. The increases in lignin concentration with accumulated mass loss for different sets of decomposing unified Scots pine needle litter incubated at five climatically different sites (Nos 2, 3:1, 6:51, 8, and 13) all of them with a mor soil. The slopes of the regression lines for sites Nos 2, 3:1, and 6:51 are significantly different from those of sites Nos 8 and 13 (cf Table 2). Further, the slopes of the line for plot 3:1 was significantly different from those of sites 6:51 and 2.

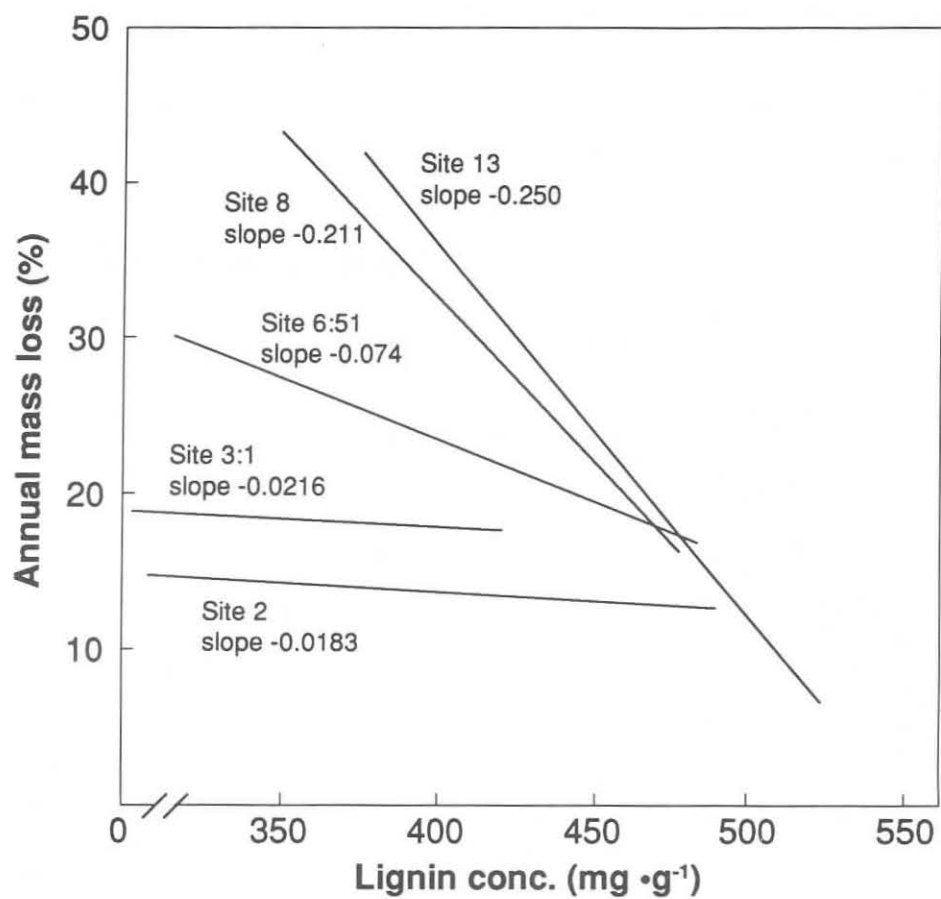


Fig 3. Linear relations for annual mass loss as dependent on lignin concentration at the start of each one-year period at five climatically different sites (Nos 2,3:1,6:51,8 and 13). The slopes for the regression lines are all significantly different.

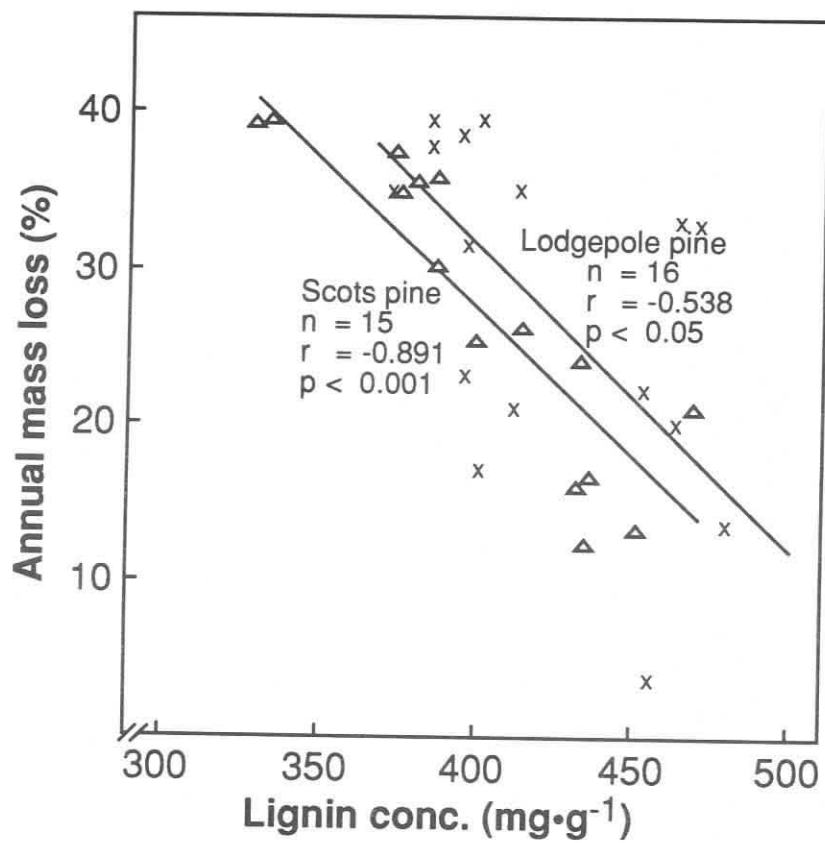


Fig 4. Linear relations between annual mass loss from decomposing lodgepole pine (x) and Scots pine ($\triangle$) needle litter and the concentration of lignin at the start of each one-year period. The regression lines are not significantly different (From Berg and Lundmark, 1985;1987)

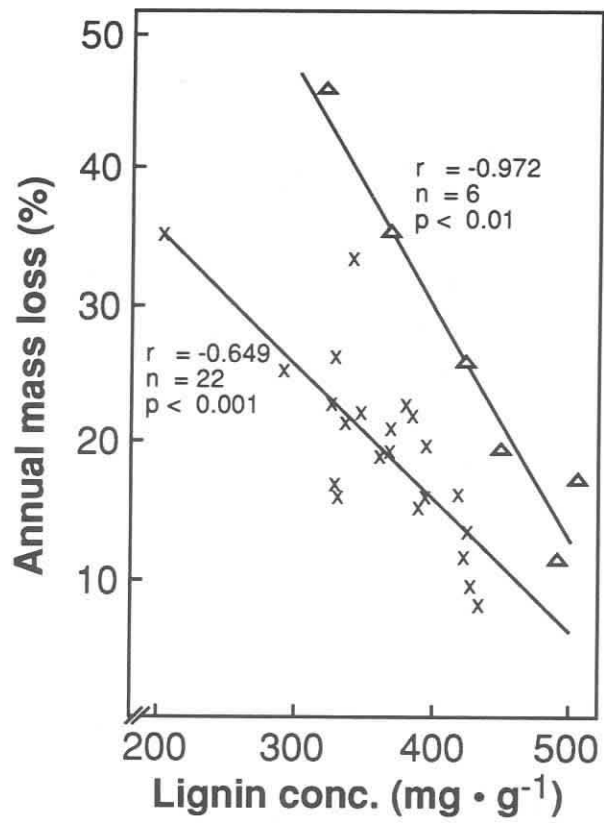


Fig 5. Annual mass loss of litter plotted versus lignin concentration at the start of each one-year period for experimental plots at site 6. Litter in control plot (x), and irrigated plus fertilized plot (Δ). Data from Berg et al., (1991c).

Table 1. Overview of site locations and climatic data. Basic data for all these sites are given by Berg et al. (1991a) and Pastor et al. (1982).

Site name	Ref No	Long/Lat	Altitude (m)	Mean annual temp. (°C)	Mean annual precip. (mm)	Soil texture	Ground vegetation type	Site descr. by
<u>Main sites</u>								
Harads	2	66°08'N;20°53'E	58	+1.3	650	Fine sand	Lichen type	(1,8,9)
Manjärvi	3:1	65°47'N;20°37'E	135	+1.0	700	Fine sand	Lichen-rich	(1,8,9)
"	3:2	65°47'N;20°37'E	"	+1.0	700	Silt	Dwarf shrub type (V.myrtillus)	(1,8,9)
"	3:3	65°47'N;20°37'E	"	+1.0	700	Silt	Low herbs type	(1,8,9)
Norrliden control	4:23	64°21'N;20°53'E	260	+1.2	595		Dwarf shrub type (V.myrtillus)	(1,3)
fertiliz.4:29*		64°21'N;20°53'E	"	"	"		Grass type (Carex)	(1,3)
Jädraås (old forest)	6:51	60°49'N;16°30'E	185	+3.8	609	Fine sand	Dwarf shrub type (V. myrtillus)	(1,2)

Table 1. Continued

Site name	Ref No	Long/Lat	Altitude (m)	Mean annual temp. (°C)	Mean annual precip. (mm)	Soil texture	Ground vegetation type	Site descr by
Jädraås (young experimental stand)								
control	6:15	"	"	"	"	Fine sand	Dwarf shrub type (V.myrtillus)	(1,2)
fert.	6:5*	"	"	"	"	"	No ground veget.	(1,2)
irrig.	6:17	"	"	"	"	"	Dwarf shrub type (V. myrtillus)	(1,2)
irrig.+ fertil.	6:4**	"	"	"	"	"	Tall herbs type	(1,2)
Nennesmo	8	58°16'N;13°35'E	155	+6.2	930		Dwarf shrub type (V.myrtillus)	(1)
Ehrhorn	13	53°00'N;09°57'E	81	+8.7	730		Grass type (Carex)	(1,9)
Malung								
M:17		60°33'N;13°44'E	375	+2.8	705	Fine sandy till	Dwarf shrub type (V.myrtillus)	(4)
M:18		60°38'N;13°37'E	400	+2.0	700	Sandy till	-"-	(4)
M:19		60°35'N;13°34'E	435	+1.8	710	Fine sandy till	Dwarf shrub type (V. myrtillus)	(4)
Lisselbo***								
LISS		60°28'N;16°57'E	80	+4.8	593	Gravelly to fine sandy till		(6,7)
Blackhawk Island								
B.I.		43°38'N;89°47'W	289	+7.6	799	Silt loam	No ground veget.	(5,10)

Table 1. Continued

Site name	Ref No	Long/Lat	Altitude (m)	Mean annual temp. (°C)	Mean annual precip. (mm)	Soil texture	Ground vegetation type	Site description
<u>Less intensively studied sites</u>								
Mästocka	10:1	56°36'N;13°15'E	"	+6.8	1070	Sandy till	Dwarf shrub type (V.myrtillus) (1,8,9)	
Skällarimsheden	100	66°32'N;20°11'E	280	-0.5	500	Sandy till	Dwarf shrub type	
Västbyn	101	63°13'N;14°28'E	325	+2.0	455	Clayey till	Dwarf shrub type (V.myrtillus) (8,9)	
Tomta	102	59°49'N;16°33'E	63	+5.0	500	Glacial clay	Grass type	(8,9)
Kungs-Husby	103	59°31'N;17°16'E	30	+5.3	470	Glacial clay	Low herbs type with dwarf shrubs	(8,9)
Dimbo	104	59°07'N;15°44'E	70	+5.5	550	Fine sand-medium sand	Grass type	(8,9)
Grensholm	105	58°33'N;15°51'E	58	+6.1	525	Glacial clay	Tall herbs type	(8,9)
Remnings-torp	106	58°28'N;13°39'E	128	+5.4	550	Glacifluvial gravel sand	Low herbs with dwarf shrubs	(8,9)
Tveten	107	58°06'N;13°17'E	170	+5.4	600	Sandy till	Dwarf shrub type (V.myrtillus) (8,9)	
Sänksjön	108	58°04'N;14°08'E	245	+5.1	595	Fine-medium sand	Lichens type	(8,9)

Table 1 (cont.)

1. Berg et al. (1986)	
2. Axelsson and Bråkenhielm (1980)	* solid fertilizer
3. Holmen et al. (1976)	
4. Berg and Lundmark (1985;1987)	** irrigation and dissolved fertilizer
5. McClaugherty and Berg (1987)	
6. Tamm et al. (1974)	*** sampling of litter only
7. Berg et al. (1987)	
8. Johansson (1986)	
9. Berg et al. (1991a)	
10. Pastor et al. (1982)	

Table 2. Slopes for the lignin concentration increase rate (LCIR) with accumulated mass-loss of decomposing, chemically similar Scots pine needle litter in natural Scots pine forests. At each site several sets of incubated litter are included in the regression (cf. Appendix 3a, 3b; Table 4). Significant differences in slope are indicated. All decomposition data available from sets of incubated litter at each site have been lumped together to one linear regression.

Site	Intercept±S.E. (mg g ⁻¹)	Slope±S.E. (LCIR) (mg % ⁻¹)	r ²	n	p	lit.ref.
Site 2	285.4 ± 34.1	2.48 ± 0.54	0.659	13	<0.001	(3)
Site 3:1	284.7 ± 12.4	1.97 ± 0.22	0.933	8	<0.001	(4)
Site 6:51	^a 261.8 ± 28.2	2.97 ± 0.11	0.869	104	<0.001	(3)
	^b 261.4 ± 21.2	3.20 ± 0.13	0.908	65	<0.001	(1,2,3)
Site 8	253.1 ± 29.4	3.90 ± 0.26	0.893	28	<0.001	(3)
Site 13	263.2 ± 28.4	4.04 ± 0.23	0.903	35	<0.001	(3)

a. Unified Scots pine needle litter

b. Scots pine needle litter from the fertilized plots of site LISS plus green Scots pine needle litter

1. Berg et al. (1982)

2. Berg and Ekbohm (1991)

3. Berg et al. (1991b)

4. Johansson (1986)

Table 3. The lignin concentration increase rate (LCIR) in decomposing Scots pine needle litter vs. accumulated litter mass-loss in locally collected litter incubated in Scots pine forests. The plots are located in a climatic transect. Maximum accumulated mass loss for the incubated litter set as well as initial lignin concentrations are given. Data from Johansson (1986) and from Berg et al. (1991b).

Site and plot		Max. acc. mass loss (%)	1st-year mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Intercept ±SE (mg g ⁻¹)	Slope ± SE (LCIR) (mg % ⁻¹)	r ²	n	p
2	Harads	51.2	11.1	254.6	281.8 ± 16.7	2.57 ± 0.37	0.891	8	<0.001
100	Skällarims- heden	48.4	17.9	244.2	278.5 ± 24.6	2.74 ± 0.61	0.823	6	<0.05
3:1	Manjärvi	66.4	19.8	271.3	284.7 ± 12.4	1.97 ± 0.22	0.932	8	<0.001
3:2	Manjärvi	78.4	25.9	272.7	290.3 ± 13.7	2.55 ± 0.21	0.962	8	<0.001
3:3	Manjärvi	78.0	30.7	268.3	270.1 ± 4.5	2.83 ± 0.07	0.996	8	<0.001
101	Västbyn	83.4	36.4	261.8	263.1 ± 15.3	2.88 ± 0.22	0.968	8	<0.001
M	Malung*	-	-	-	277.5 ± 19.7	2.53 ± 0.11	0.907	54	<0.001
6:51	Jädraås**	-	-	-	261.8 ± 28.2	2.88 ± 0.11	0.869	104	<0.001
102	Tomta	79.7	36.9	254.5	278.5 ± 25.3	3.31 ± 0.37	0.919	9	<0.001
103	Kungs-Husby	69.8	38.1	225.8	227.8 ± 14.9	4.06 ± 0.25	0.982	7	<0.001
104	Dimbo	80.8	43.7	246.0	269.1 ± 24.9	3.30 ± 0.36	0.922	8	<0.001
105	Grensholm	73.1	42.0	218.8	235.8 ± 20.6	3.91 ± 0.34	0.971	6	<0.001
106	Remnings- torp	79.1	35.2	254.5	258.4 ± 13.5	3.36 ± 0.19	0.979	9	<0.001
107	Tveten	73.8	36.3	347.5	330.9 ± 24.6	2.14 ± 0.41	0.901	5	<0.01
108	Sänksjön	63.9	30.0	230.5	241.2 ± 14.2	3.57 ± 0.23	0.972	9	<0.001
10:1	Mästocka	73.5	42.2	281.2	274.7 ± 16.1	3.08 ± 0.24	0.966	8	<0.001
4:23	Norrliden	51.2	17.4	284.4	290.4 ± 12.6	3.05 ± 0.22	0.953	11	<0.001

* average slope of 5 incubations (cf Table 8)

** average slope of 12 incubations (cf Table 2)

Table 4. Slopes for increase in lignin concentration vs. accumulated mass-loss (LCIR) for local litter in three nearby natural plots within one site (No 3, Manjärv). The plots had different vegetation and soil types. Significant differences are indicated. Data from Johansson (1986).

Plot No	Intercept $\pm$ SE (mg g ⁻¹)	Slope $\pm$ SE (mg % ⁻¹)	r ²	n	p
1	284.7 $\pm$ 12.4	^a 1.97 $\pm$ 0.22	0.933	8	<0.001
2	290.3 $\pm$ 13.7	^b 2.55 $\pm$ 0.21	0.962	8	<0.001
3	270.1 $\pm$ 4.5	^b 2.83 $\pm$ 0.07	0.996	8	<0.001

a Significantly different from b-labelled slope

b Significantly different from a-labelled slope

Table 5. The increase in lignin concentration in decomposing Scots pine needles versus accumulated mass-loss (LCIR) in experimental Scots pine plantations. Basic data in Appendix 4 and publ. by Berg et al. (1991b)

Site/plot	Intercept $\pm$ SE (mg g ⁻¹)	Slope $\pm$ SE (LCIR) (mg % ⁻¹)	r ²	n	p
<u>Site 4 (Norrliden)</u>					
Plot 4:23 (control)					
green needles	212.4 $\pm$ 20.1	^a 5.27 $\pm$ 0.29	0.962	15	<0.001
brown needles	276.0 $\pm$ 27.9	^c 2.99 $\pm$ 0.28	0.802	30	<0.001
green + brown	255.7 $\pm$ 32.6	^a 3.77 $\pm$ 0.28	0.821	45	<0.001
Plot 4:29 (fertilized*)					
green needles	211.8 $\pm$ 28.6	^a 5.17 $\pm$ 0.12	0.993	14	<0.001
brown needles	261.1 $\pm$ 24.2	^d 4.25 $\pm$ 0.22	0.915	37	<0.001
green + brown	249.9 $\pm$ 23.2	^b 4.47 $\pm$ 0.17	0.929	51	<0.001
<u>Site 6 Jädraås</u>					
Plot 6:15 (control)					
brown needles	271.0 $\pm$ 17.7	^a 3.21 $\pm$ 0.29	0.922	12	<0.001
Plot 6:17 (irrigated)					
brown needles	245.3 $\pm$ 12.5	^a 3.05 $\pm$ 0.26	0.966	7	<0.001
6:5 (fertilized)**					
brown needles	254.1 $\pm$ 14.2	^a 3.57 $\pm$ 0.27	0.963	9	<0.001
6:4 (irr.+fert.)***					
brown needles	260.3 $\pm$ 16.2	^b 4.87 $\pm$ 0.28	0.974	10	<0.001

Table 5 (cont)

- a significantly different from b-labelled slope within the same site
- b significantly different from a-labelled slope within the same site
- c significantly different from d-labelled slope within the same site
- d significantly different from c-labelled slope within the same site
- e indicated values are significantly different
- * fertilized with N and P (solid fertilizer)
- ** fertilized with N (solid fertilizer)
- *** irrigated and fertilized - balanced mixture of fertilizer dissolved in water

Table 6 . Linear regressions for LCIR values versus initial lignin concentration and first-year mass-loss (data from Table 3 and Appendix 3) for a wide range of climatically different sites and leaf and needle litters. n.s. stands for "not significant", all other relations were highly significant ($p < 0.001$).

	Intercept $\pm$ SE (mg g ⁻¹)	Slope $\pm$ SE (mg % ⁻¹)	r ²	n	p
<u>Local Scots pine needle litter from a climatic transect</u>					
LCIR vs. 1st-year mass-loss					
	1.89 $\pm$ 0.52	0.036 $\pm$ 0.015	0.330	14	<0.05
LCIR vs. initial lignin conc.					
	6.78 $\pm$ 0.43	-0.014 $\pm$ 0.004	0.546	14	<0.01
LCIR vs. initial lignin conc. and 1st-year mass-loss					
	5.62 $\pm$ 0.25	-0.014 $\pm$ 0.002(lig) 0.034 $\pm$ 0.006 (m.l.)	0.863	14	<0.001
Initial lignin conc vs 1-st year mass loss			0.000	14	n.s.
<u>All unified and local Scots pine and white pine needle litters in natural systems</u>					
LCIR vs. 1st-year mass-loss					
	2.185 $\pm$ 0.658	+0.0334 $\pm$ 0.014	0.111	47	<0.05
LCIR vs. initial lignin conc.					
	6.820 $\pm$ 0.572	-0.0141 $\pm$ 0.003	0.387	47	<0.001
LCIR vs. initial lignin conc. and 1st-year mass-loss					
	5.761 $\pm$ 0.544	-0.0135 $\pm$ 0.0029(lig) +0.0281 $\pm$ 0.0117(m.l.)	0.406	47	<0.001
Initial lignin conc. vs 1st-year mass loss			0.010	47	n.s.

Table 7. A comparison of the rate-regulating effect of lignin in some sets of chemically different pine needle litters incubated at site No 6:51, site B.I. and site M. Basic data published by Berg et al. (1991b).

Litter sp. type	Slope±SE (mg % ⁻¹)	Equation		Intercept±SE (mg g ⁻¹)		r ²	n
<u>Site 6</u>							
Control plot 6:51 Scots pine (unified)*	-0.078	0.016	54.86	3.46	0.478	29	
Scots pine (exper)	-0.085	0.016	58.634	3.01	0.633	18	
Control plot 6:15 Scots pine	-0.095	0.019	55.29	2.80	0.652	16	
Irr.+fert plot 6:4 Scots pine	-0.116	0.025	91.71	3.17	0.849	9	
<u>Site M</u>							
Scots pine	-0.190	0.027	103.95	4.50	0.801	14	
Lodgepole pine	-0.189	0.071	106.59	9.29	0.371	14	

*. At this site the unified litter also was the local litter

Table 8. Increase in lignin concentration (LCIR) with accumulated mass-loss (Appendix 3a, 3c) of different decomposing litter types compared at single sites. Different letters as indices on slopes mark significant site-specific differences. Basic data in Appendix 3a,3c, and 4.

Site and litter type	Intercept ± SE (mg g ⁻¹)		Slope ± SE (LCIR) (mg % ⁻¹)		r ²	n	p	Basic inform. in lit ref.
Natural systems - local litter								
<u>Site M</u>								
Scots pine	277.5	19.70	^a 2.55	0.11	0.907	54	<0.001	(2)
lodgepole pine	370.6	23.61	^b 1.24	0.13	0.617	55	<0.001	(2)
Natural systems - transplanted litter								
<u>Site 6:51</u>								
Lodgepole pine needles								
green	374.4	13.25	1.71	0.19	0.881	13	<0.001	(1)
brown	386.0	10.21	1.35	0.13	0.902	13	<0.001	(1)
<u>Site B.I.</u>								
White pine	240.1	10.70	^a 3.12	0.15	0.977	13	<0.001	(3)
Eastern hemlock	222.1	20.08	^b 3.97	0.32	0.932	13	<0.001	(3)

Table 8 continued

Site and litter type	Intercept $\pm$ SE (mg g ⁻¹)		Slope $\pm$ SE (LCIR) (mg % ⁻¹)		r ²	n	p	Basic inform. in lit ref.
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Experimentally modified systemsSite 4

Scots pine needles

plot 4:23,	^c 255.7	32.6	^a 3.77	0.27	0.821	45	<0.001	(4)
plot 4:29,	^c 249.9	23.2	^b 4.47	0.18	0.929	51	<0.001	(4)

a significantly different from "b-labelled" slopes within the same site.

b significantly different from "a-labelled" slope within the same site.

c all incubated brown needle litter

(1) Berg and Ekbohm (1991)

(2) Berg and Lundmark (1985;1987)

(3) Aber et al. (1986)

(4) Berg et al. (1991c)

Appendix 1. Initial chemical composition of the unified Scots pine needle litter collected at the same site (No 6) annually over a 14-year period. n.d. stands for "not determined".

Collection year	Concentration of component (mg g ⁻¹)										
	water solub.	ethanol solub.	lignin	N	P	S	K	Ca	Mg	Mn	Ash
1973	92	120	223	3.8	0.19	0.42	0.73	6.5	0.38	1.55	23
1974	145	84	270	4.2	0.22	0.29	0.71	5.4	0.49	n.d.	24
1975	172	107	238	3.4	0.20	0.32	0.61	4.7	0.39	n.d.	19
1976	151	89	255	4.0	0.21	0.36	0.53	4.9	0.42	n.d.	n.d.
1977	202	102	224	4.1	0.19	0.38	0.87	6.0	0.42	1.02	n.d.
1978	164	96	257	3.8	0.2	0.33	0.62	5.5	0.55	1.00	20
1979	129	95	286	10.4	0.29	0.78	0.97	2.3	0.39	0.31	12
1980	180	102	246	3.8	0.18	5.4	1.72	6.1	0.53	0.77	21
1981	213	94	231	3.9	0.28	0.61	1.02	7.1	0.58	1.17	23
1982	164	113	231	4.8	0.33	0.55	1.07	4.4	0.49	0.79	26
1983	178	112	229	3.8	0.30	0.45	0.90	5.9	0.39	1.08	n.d.
1984	82	116	288	3.7	0.21	n.d.	0.82	6.3	0.44	0.12	23
1985	182	94	241	3.0	0.19	0.45	0.52	4.8	0.38	1.24	18
1986	170	89	257	4.0	0.23	0.44	0.58	5.6	0.57	1.13	n.d.

Appendix 2. Initial chemical composition of locally collected leaf and needle litters used in the study. The appendix also serves as an overview to where local litter was incubated. Unified litter was collected at site No 6.

Collection Litter type site and plot		Concentration of component (mg g ⁻¹)											lit.
		water solub.	ethanol solub.	lignin	N	P	S	Mg	Ca	K	Mn	Ash	
<u>No 2 (Harads)*</u>													
Scots pine needles													
	brown needles	n.d.	n.d.	255	4.11	0.34	n.d.	0.52	5.83	0.91	0.37	n.d.	(5)
<u>No. 3 (Manjärv)**</u>													
Scots pine needles													
3:1	brown needles	n.d.	n.d.	271	2.94	0.21	n.d.	0.66	6.40	0.55	1.17	n.d.	(1,5)
3:2	" "	n.d.	n.d.	273	3.05	0.21	n.d.	0.79	7.04	0.38	1.15	n.d.	(1,5)
3:3	" "	n.d.	n.d.	268	3.24	0.21	n.d.	0.81	9.28	0.71	1.22	n.d.	(1,5)
<u>No 4 (Norrliden)*</u>													
Scots pine needles													
4:23 (control plot)													
	brown needles	93	96	284	2.47	0.27	0.51	0.52	6.47	0.66	1.37	n.d.	(1,2)
	green needles	200	62	212	14.00	1.62	n.d.	0.78	2.40	5.09	0.84	n.d.	(1,2)
4:29 (fertilized)													
	brown needles	91	94	282	n.d.	n.d.	n.d.	n.d.	4.36	n.d.	n.d.	n.d.	(1,2)

Appendix 2 (continued)

Collection Litter type		Concentration of component (mg g ⁻¹)											
site and plot		water solub.	ethanol solub.	lignin	N	P	S	Mg	Ca	K	Mn	Ash	lit.
<u>No 6 (Jädraås)</u> (local litters)													
6:51 Scots pine needles													
brown needles				"Unified" litter - see Appendix 1									
green needles	180	90	220	15.1	1.31	1.13	0.82	2.77	4.67	0.26	n.d.	(1,3)	
<u>Experimental stands</u> (no local litter incubated)													
6:15 control	213	94	231	3.9	0.28	0.61	0.58	7.08	1.02	1.17	n.d.	(1,2)	
6:17 irrigated	164	94	231	4.8	0.33	0.55	0.49	4.42	0.79	1.07	n.d.	(1,2)	
6:5 fertilized	164	113	231	4.8	0.33	0.55	0.49	4.42	0.79	1.07	n.d.	(1,2)	
6:4 irrigated and fertilized	213	94	231	3.9	0.28	0.61	0.58	7.08	1.02	1.17	n.d.	(1,2)	
<u>No. 8 (Nennesmo)</u> (no local litter)***													
<u>No. 13 (Ehrhorn)</u> (no local litter)***													
<u>M (Malung)</u> (local litter only)**													
M:17 lodgepole pine needles													
brown needles	69	46	289	3.4	0.31	n.d.	0.88	6.8	0.40	2.19	n.d.	(1,6)	
" "	109	47	366	4.0	0.44	n.d.	1.06	9.07	0.52	3.07	n.d.	(1,6)	
" "	103	42	381	3.9	0.34	0.62	0.95	6.35	0.56	1.79	n.d.	(1,6)	
green "	147	36	346	10.5	0.82	1.17	0.93	3.99	3.84	0.82	n.d.	(1,6)	

Appendix 2 (continued)

[illegible]

[illegible]

1. Berg et al. (1991b) * local and unified litter incubated
2. Berg et al. (1991 c) ** only local litter incubated
3. Berg and Ekbohm, (1991) *** only unified litter incubated
4. Berg and Wessén (1984)
5. Johansson (1986)
6. Berg and Lundmark (1985;1987)
7. McClaugherty (199X)

Appendix 3 a. The linear increase in lignin concentration as compared to accumulated mass loss (LCIR) at the main Jädraås site (6:51). Initial lignin concentration and max. accumulated mass losses are also given.

Incubation date	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Interercept ± SE (mg g ⁻¹)	Slope ± SE (LCIR) (mg % ⁻¹)	r ²	n	p	lit ref
<u>Unified Scots pine needles</u>								
740502	77.1	223	254±21.2	3.19±0.22	0.929	18	<0.001	(1,2,3,6)
741023	58.1	270	288±16.5	2.30±0.36	0.889	7	<0.001	(2,3,6)
761111	67.5	267	251±12.8	3.36±0.21	0.972	9	<0.001	(2,3,6)
761027	65.1	224	256±29.1	2.78±0.55	0.865	6	<0.001	(2,3,6)
781113	68.1	257	270±19.0	2.98±0.37	0.970	4	<0.001	(6)
821004	63.2	288	316±23.0	2.76±0.41	0.882	8	<0.001	(6)
821102	67.4	236	253±13.9	2.78±0.19	0.953	12	<0.001	(6)
831027	65.5	229	248±15.3	2.85±0.25	0.947	10	<0.001	(6)
840523	70.2	229	230± 9.8	3.12±0.14	0.983	11	<0.001	(6)
841030	59.0	288	250±16.3	3.45±0.27	0.952	10	<0.001	(6)
850522	53.1	288	250±15.4	3.81±0.28	0.963	9	<0.001	(6)
<u>experimental and green Scots pine needles</u>								
761111	68.8	256	264± 9.7	3.20±0.14	0.985	10	<0.001	(4,6)
761111	67.7	251	257± 9.6	3.47±0.14	0.987	10	<0.001	(4,6)
761111	70.4	269	285±10.7	3.03±0.16	0.979	10	<0.001	(4,6)
761111	67.6	268	286±12.6	3.07±0.19	0.970	10	<0.001	(4,6)
821102*	65.9	220	250±16.9	3.16±0.26	0.936	12	<0.001	(5,6)
830817	58.2	208	255±21.9	2.77±0.35	0.852	13	<0.001	(6)

Appendix 3a (continued)

Incubation date	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Interercept ± SE (mg g ⁻¹)	Slope ± SE (LCIR) (mg % ⁻¹)	r ²	n	p	lit ref
<u>lodgepole pine needles</u>								
821102*	66.0	346	374±13.2	1.71±0.19	0.881	13	<0.001	(5,6)
821102	63.1	381	386±10.2	1.35±0.13	0.902	13	<0.001	(5,6)

-
- | | |
|----------------------------|---------------------------|
| 1. Berg et al. (1982) | 5. Berg and Ekbohm (1991) |
| 2. Jansson and Berg (1985) | 6. Berg et al. (1991b) |
| 3. Berg and Ågren (1984) | |
| 4. Berg et al. (1987) | |

* green litter

Appendix 3b. The rate of increase (LCIR) for lignin concentration in decomposing Scots pine needle litter as compared to accumulated mass loss at sites Nos 2 (Harads), 8 (Nennesmo) and 13 (Ehrhorn). Standard errors are given after intercept and slope.

Site and incubation date	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Intercept (mg g ⁻¹)	Slope (LCIR) (mg % ⁻¹)	r ²	n	p	lit ref
<u>No 2 (Harads)</u>								
local litter 790706	51.2	254.6	281.8 ± 16.66	2.57 ± 0.37	0.891	8	<0.01	(1)
unified litter 830613	49.6	232.1	231.6 ± 2.05	3.25 ± 0.06	0.999	5	<0.001	(2)
exp. litter 830613	48.1	284.2	274.3 ± 18.79	3.67 ± 0.51	0.962	5	<0.01	(2)
<u>No 8 (Nennesmo)</u>								
unified litter 810119	59.4	246.1	263.6 ± 31.18	4.29 ± 0.70	0.950	4	<0.05	(2)
821119	58.5	231.3	250.4 ± 0.49	4.38 ± 0.49	0.952	6	<0.01	(2)
831108	57.7	231.4	254.0 ± 23.09	3.74 ± 2.52	0.946	5	<0.01	(2)
840508	63.6	222.6	225.6 ± 4.92	3.47 ± 0.11	0.998	4	<0.01	(2)
841111	53.0	222.6	238.0 ± 15.90	4.27 ± 0.39	0.976	5	<0.001	(2)
850506	59.3	287.6	294.2 ± 10.07	2.57 ± 0.25	0.982	4	<0.01	(2)
exp. litter 831108	51.8	264.9	276.0 ± 11.10	3.87 ± 0.26	0.986	5	<0.001	(2)

Appendix 3b cont.

Site and incubation date	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Intercept (mg g ⁻¹)	Slope (LCIR) (mg % ⁻¹)	r ²	n	p	lit ref
<u>No 13 (Ehrhorn)</u>								
unified litter								
811029	56.1	246.1	245.0 ± 2.78	5.07 ± 0.06	1.000	5	<0.001	(2)
840604	59.5	228.6	229.9 ± 8.39	3.78 ± 0.18	0.993	5	<0.001	(2)
841107	56.9	228.6	241.2 ± 14.23	4.44 ± 0.30	0.986	5	<0.001	(2)
851107	55.2	287.6	304.1 ± 17.39	3.27 ± 0.40	0.956	5	<0.001	(2)
860603	54.3	287.6	296.7 ± 9.61	3.62 ± 0.22	0.989	5	<0.001	(2)
861106	58.4	240.7	259.0 ± 18.94	4.29 ± 0.40	0.975	5	<0.001	(2)
850521	59.4	228.6	246.8 ± 23.06	4.09 ± 0.51	0.956	5	<0.001	(2)

-
1. Johansson (1986)
 2. Berg et al. (1991b)

* not significant

Appendix 3c. The linear increase in lignin concentration as compared to accumulated mass loss (LCIR) at sites M (Malung) and B.I. (Blackhawk Island).

Site and incubation date	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Intercept ± SE (mg g ⁻¹)	Slope ± SE (LCIR) (mg % ⁻¹)	r ²	n	p	lit. ref.
<u>Site M</u>								
Scots pine								
780525	75.5	285	267.2 ± 16.1	2.59 ± 0.20	0.949	11	<0.001	(1,2)
780525	72.9	293	260.8 ± 17.6	2.60 ± 0.22	0.938	11	<0.001	(1,2)
781113	73.2	265	279.6 ± 14.1	2.67 ± 0.18	0.956	12	<0.001	(1,2)
781113	68.7	300	309.8 ± 8.3	2.02 ± 0.13	0.977	8	<0.001	(1,2)
781113	73.9	243	272.9 ± 23.6	2.77 ± 0.29	0.898	12	<0.001	(1,2)
Lodgepole pine								
780525	71.7	389	372.1 ± 16.5	0.87 ± 0.20	0.675	11	<0.001	(1,2)
780525	68.9	391	369.3 ± 23.6	0.94 ± 0.31	0.505	11	<0.001	(1,2)
781113	75.3	366	369.1 ± 23.9	1.30 ± 0.20	0.669	12	<0.001	(1,2)
781113	66.8	357	370.3 ± 16.6	1.37 ± 0.25	0.817	9	<0.001	(1,2)
781113	70.6	365	375.6 ± 17.8	1.57 ± 0.22	0.838	12	<0.001	(1,2)
<u>Site B.I.</u>								
White pine	59.5	225	240.1 ± 10.7	3.12 ± 0.15	0.977	13	<0.001	(3)
Eastern hemlock	59.2	206	222.1 ± 20.1	3.97 ± 0.32	0.932	13	<0.001	(3)

1. Berg and Lundmark (1985; 1987)
2. Berg et al. (1991b)
3. Aber et al. (1984)

Appendix 3d. The linear increase in lignin concentration in decomposing Scots pine needle litter as compared to accumulated mass loss, (LCIR) on some experimental plots of the Jädraås site (No 6). Initial lignin concentration and maximum accumulated mass loss are also given. All incubations were made on Nov 2, 1982.

Plot No	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Intercept±SE (mg g ⁻¹)	Slope±SE (LCIR) (mg % ⁻¹)	r ²	n	p	lit ref
6:15 (control)								
	61.2	231.3	271.0 ± 17.69	3.21 ± 0.29	0.922	12	<0.001	(1;2)
6:17 (irrigated)								
	57.4	231.3	245.3 ± 12.47	3.05 ± 0.26	0.966	7	<0.001	(1;2)
6:5 (fertilized)								
	58.3	231.3	254.2 ± 14.15	3.57 ± 0.27	0.963	9	<0.001	(1;2)
6:4 (irrigated and fertilized)								
	49.7	231.3	260.3 ± 16.15	4.87 ± 0.28	0.974	10	<0.001	(1;2)

1. Berg et al. (1991b)
2. Berg et al. (1991c)

Appendix 3c. The linear increase in lignin concentration as compared to accumulated mass loss (LCIR) at sites M (Malung) and B.I. (Blackhawk Island).

Site and incubation date	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Intercept ± SE (mg g ⁻¹)	Slope ± SE (LCIR) (mg % ⁻¹)	r ²	n	p	lit. ref.
<u>Site M</u>								
Scots pine								
780525	75.5	285	267.2 ± 16.1	2.59 ± 0.20	0.949	11	<0.001	(1,2)
780525	72.9	293	260.8 ± 17.6	2.60 ± 0.22	0.938	11	<0.001	(1,2)
781113	73.2	265	279.6 ± 14.1	2.67 ± 0.18	0.956	12	<0.001	(1,2)
781113	68.7	300	309.8 ± 8.3	2.02 ± 0.13	0.977	8	<0.001	(1,2)
781113	73.9	243	272.9 ± 23.6	2.77 ± 0.29	0.898	12	<0.001	(1,2)
Lodgepole pine								
780525	71.7	389	372.1 ± 16.5	0.87 ± 0.20	0.675	11	<0.001	(1,2)
780525	68.9	391	369.3 ± 23.6	0.94 ± 0.31	0.505	11	<0.001	(1,2)
781113	75.3	366	369.1 ± 23.9	1.30 ± 0.20	0.669	12	<0.001	(1,2)
781113	66.8	357	370.3 ± 16.6	1.37 ± 0.25	0.817	9	<0.001	(1,2)
781113	70.6	365	375.6 ± 17.8	1.57 ± 0.22	0.838	12	<0.001	(1,2)
<u>Site B.I.</u>								
White pine	59.5	225	240.1 ± 10.7	3.12 ± 0.15	0.977	13	<0.001	(3)
Eastern hemlock	59.2	206	222.1 ± 20.1	3.97 ± 0.32	0.932	13	<0.001	(3)

1. Berg and Lundmark (1985; 1987)
2. Berg et al. (1991b)
3. Aber et al. (1984)

Appendix 3d. The linear increase in lignin concentration in decomposing Scots pine needle litter as compared to accumulated mass loss, (LCIR) on some experimental plots of the Jädraås site (No 6). Initial lignin concentration and maximum accumulated mass loss are also given. All incubations were made on Nov 2, 1982.

Plot No	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Intercept±SE (mg g ⁻¹)	Slope±SE (LCIR) (mg % ⁻¹)	r ²	n	p	lit ref
6:15 (control)								
	61.2	231.3	271.0 ± 17.69	3.21 ± 0.29	0.922	12	<0.001	(1;2)
6:17 (irrigated)								
	57.4	231.3	245.3 ± 12.47	3.05 ± 0.26	0.966	7	<0.001	(1;2)
6:5 (fertilized)								
	58.3	231.3	254.2 ± 14.15	3.57 ± 0.27	0.963	9	<0.001	(1;2)
6:4 (irrigated and fertilized)								
	49.7	231.3	260.3 ± 16.15	4.87 ± 0.28	0.974	10	<0.001	(1;2)

1. Berg et al. (1991b)
2. Berg et al. (1991c)

Appendix 4. The increase rate for lignin concentration in decomposing Scots pine needle litter (LCIR) as compared to accumulated mass-loss on two experimental plots at site No4 (Norrliden). Data from Berg et al. (1991b,c)

Incubation date	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Intercept ±SE (mg g ⁻¹)	Slope±SE (LCIR) (mg % ⁻¹)	r ²	n	p
<u>Plot 4:23 (control)</u>							
Unified litter							
830607	60.9	231.4	237.4 ± 8.2	3.38 ± 0.13	0.987	11	<0.001
840605	47.7	228.6	275.7 ± 38.2	3.43 ± 0.90	0.706	8	<0.01
Local litter							
830607	51.2	284.4	290.4 ± 12.6	3.05 ± 0.22	0.953	11	<0.001
Experimental litter							
840605*	55.5	211.9	212.7 ± 7.0	5.15 ± 0.14	0.996	8	<0.001
840911*	53.21	211.9	210.0 ± 30.0	5.50 ± 0.63	0.938	7	<0.001
<u>Plot 4:29 (fertilized)</u>							
Unified litter							
830607	60.02	231.4	228.1 ± 10.1	4.37 ± 0.16	0.989	11	<0.001
840605	49.27	228.6	251.7 ± 16.5	4.93 ± 0.38	0.966	8	<0.001
840911	47.58	228.6	242.1 ± 10.1	4.90 ± 0.24	0.988	7	<0.001

Appendix 4 (continued)

Incubation date	Max. acc. mass loss (%)	Initial lignin conc. (mg g ⁻¹)	Intercept ±SE (mg g ⁻¹)	Slope±SE (LCIR) (mg % ⁻¹)	r ²	n	p
Local litter							
830607	51.20	282.1	286.4 ± 9.2	4.15 ± 0.16	0.986	11	<0.001
Experimental litter							
840605*	58.66	211.9	214.5 ± 10.0	5.12 ± 0.19	0.992	8	<0.001
840911*	54.48	211.9	208.9 ± 8.3	5.23 ± 0.18	0.995	6	<0.001
* green needle litter							